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HISTORICAL BIOGEOGRAPHY OF THE ASTERACEAE FROM TANDILIA AND VENTANIA MOUNTAIN RANGES (BUENOS AIRES, ARGENTINA)

A nuestra amiga Pilar

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ABSTRACT

Tandilia and Ventania are the only systems of mountain ranges situated in a grassy steppe or "pampas" in the political province of Buenos Aires in Argentina. Tandilia and Ventania have a high taxa diversity and endemicity. A historical biogeographic analysis was carried out on the basis of distributional patterns of species and infraspecific taxa of Asteraceae inhabiting Tandilia and Ventania in order to establish the relationships of these mountain ranges with other areas. Two methods were applied for the analysis: panbiogeography using the compatibility track method and parsimony analysis of endemicity (PAE). Thirteen areas were delimited for the study: Southern North America and Central America, Southern Brazil, Uruguay, Pampa, Tandilia, Ventania, Chaco, Sierras Pampeanas, Sierras Subandinas, Mahuidas, Patagonia, Central Chile, and Northern Andes. The units of the study were 112 taxa inhabiting Tandilia and Ventania (endemic, naturalized, and adventicious species were not included). Both methods connect southern Brazil, Uruguay, Pampa, Tandilia, Ventania, and Sierras Pampeanas, showing that the Asteraceae biota of Tandilia and Ventania have closer relationships with the biota of these areas rather than with that of Sierras Subandinas, North Andean, Chaco, Patagonia, Mahuidas, and Central Chile. The Asteraceae of Central and North America appear less related to Tandilia and Ventania in regard of the rest of the areas. The evolution of Asteraceae in Tandilia and Ventania and related areas is hypothetized to have been affected mainly by Tertiary and

Quaternary geologic events. The discontinuous pattern found, occurring mostly in elevated areas, is explained principally by vicariance under dry conditions.

Key words. Asteraceae; biogeography; Tandilia; Ventania.

RESUMEN

Las sierras septentrionales, o de Tandilia y las australes, o de Ventania, caracterizadas por su gran diversidad orgánica y su alto número de endemismos, están ubicadas en la planicie bonaerense de pastizales denominada "pampa". Con el objeto de establecer las relaciones entre Tandilia y Ventania con otras áreas, se analizaron las distribuciones de los taxones específicos e infraespecíficos de Asteraceae que habitan estas sierras. Se delimitaron trece áreas: sur de América del Norte y América Central, sur de Brasil, Uruguay, Pampa, Tandilia, Ventania, Chaco, Sierras Pampeanas, Sierras Subandinas, Mahuidas, Patagonia, Chile Central, y Andes del Norte. Las unidades de estudio fueron 112 taxones de Asteraceae presentes en Tandilia y Ventania (taxones endémicos, adventicios y naturalizados no fueron incluidos en el análisis). Las distribuciones de estos taxones fueron analizadas utilizando dos métodos: panbiogeografía (compatibilidad de trazos) y análisis de simplicidad de endemismos. Ambos métodos conectan sur de Brasil, Uruguay, Pampa, Tandilia, Ventania y Sierras Pampeanas. Las Asteraceae de Tandilia y Ventania estarían más relacionadas con estas áreas que con la de las Sierras Subandinas, Andes del Norte, Chaco, Patagonia, Mahuidas y Chile Central. El área de América del Norte y América Central aparece menos relacionada a Tandilia y Ventania en relación a las otras áreas. La evolución de las Asteraceae de Tandilia y Ventania y las áreas relacionadas ha sido probablemente afectada por los eventos geológicos de los períodos Terciario y Cuaternario. La discontinuidad actual en el patrón de distribución de las Asteraceae, restringidas en general a las zonas elevadas, es explicada principalmente por eventos vicariantes debidos a condiciones áridas.

Palabras clave. Asteraceae; biogeografía; Tandilia; Ventania.

INTRODUCTION

Since Darwin's journey in Argentina in 1835 the geology of Tandilia and Ventania and their inhabiting biota have attracted several generations of geologists and biologists (e.g., Darwin 1846, Alboff 1895, Hauthal 1901, Cabrera 1938, Sota 1967, Teruggi & Kilmurray 1975). The political province of Buenos Aires, situated in central eastern Argentina, is covered in most of its surface by an herbaceous, grassy steppe, called "pampas". The pampas are a plain situated at the sea level, or even below the sea level (like the big depression of the Salado river), with the exception of two major systems of mountains ranges or "sierras", namely Tandilia and Ventania.

From a geological point of view, Tandilia and Ventania do not appear to be very closely related (Rolleri 1975). Tandilia, southeastern of Buenos Aires province, constitutes the oldest nucleus in the country originated in the Proterozoic age. Ventania is located southwest of the province and has a more recent origin dated from the Paleozoic age. Gondwanaland and Pre-Gondwanaland events seem to have played a major role in the building of these mountain ranges.

The biodiversity of Tandilia and Ventania is particularly interesting because of their high number of endemic plantae and animal taxa (Table 1), and led to consider the ranges as "orographic islands" (Kristensen & Frangi 1995). When compared with the remaining vegetation of Buenos Aires, Tandilia and Ventania have not only a characteristic petrophylous flora, but they are the only regions in the province with endemic plant taxa (Parodi 1947). There have been numerous floristic (Alboff 1895, Spegazzini 1896, 1901, Cabrera 1938, 1940, 1963) and ecological (Frangi 1973, Ponce 1982, 1986, Kristensen & Frangi 1995) studies in the area. The different communities were explained by the variation in the local climate and soil, which is caused by aspects of the topography of the ranges (Kristensen & Frangi 1995).

Within the diverse plant families inhabiting Tandilia and Ventania, Asteraceae have the second place (after Poaceae, the grass family) in number of genera and species represented in the area (Parodi 1947). Approximately 30 % (112 species and infraspecific taxa) out of the 356 Asteraceae known from the Buenos Aires province (Cabrera 1963, Zuloaga & Morrone 1999, Cabrera et al. 2000) occur in Ventania and Tandilia. Furthermore, there have been found until the present four species of Asteraceae endemic to Tandilia, three species and two varieties endemic to Ventania, and one species endemic to both, Tandilia and Ventania.

The current understanding of the biotic history of Tandilia and Ventania is based on several lines of evidence. Systematic studies have documented much of the taxonomic diversity and distribution patterns of ferns (Sota 1967, 1972, 1973, 1985) and scorpions (Maury 1973) and some hypotheses were postulated to explain those distributions.

It would be interesting to seek the historical explanations that led to the high diversity and endemicity of Asteraceae in Tandilia and Ventania and the relationships of the biota inhabiting these mountain ranges with other areas. In order to achieve this goal, we apply herein two methods: a panbiogeographic approach (compatibility track analysis) and parsimony analysis of endemicity (Morrone & Crisci 1990, 1995, Crisci et al. 2000) based on distributional patterns exhibited by Asteraceae.

MATERIAL AND METHODS

Areas

Except for a few weedy introductions (e.g., *Facelis retusa*, *Gamochaeta subfalcata*), the Asteraceae of this region shows no links outside of the Americas. For these reason, areas such as Palearctic, Afrotropical, Oriental, Australian, Cape subregions, were not taken into consideration for the delimitation areas.

On the basis of several overlapping taxa distribution and phytogeographical and geological criteria the areas delimited here are (Fig. 1):

(1) *Central Chile* (CHI): Chile between 30° and 37° south latitude (Cabrera & Willink 1973, Morrone et al. 1997).
(2) *Central and North America* (CNA): Southern North America and Central America.
(3) *Chaco* (CHA): xerophyllous forest extending from southern Bolivia, western Paraguay, and northern and central Argentina (Cabrera & Willink 1973).
(4) *Mahuidas* (MA): group of mountain ranges in the political province of La Pampa, in central Argentina. They are 300-500 m high, and they are dated from the Cambric age (500 m. y. ago) (Zambrano 1980).
(5) *Northern Andes* (NA): corresponds to the Paramo and Puna provinces, and comprises the highlands over 3000 m altitude from Venezuela to northwestern Argentina (Morrone 1994).
(6) *Pampa* (PAM): grassy steppe ranging from southern Brazil, Uruguay, and eastern Argentina, from 30° south latitude to 39° south latitude (Cabrera & Willink 1973).

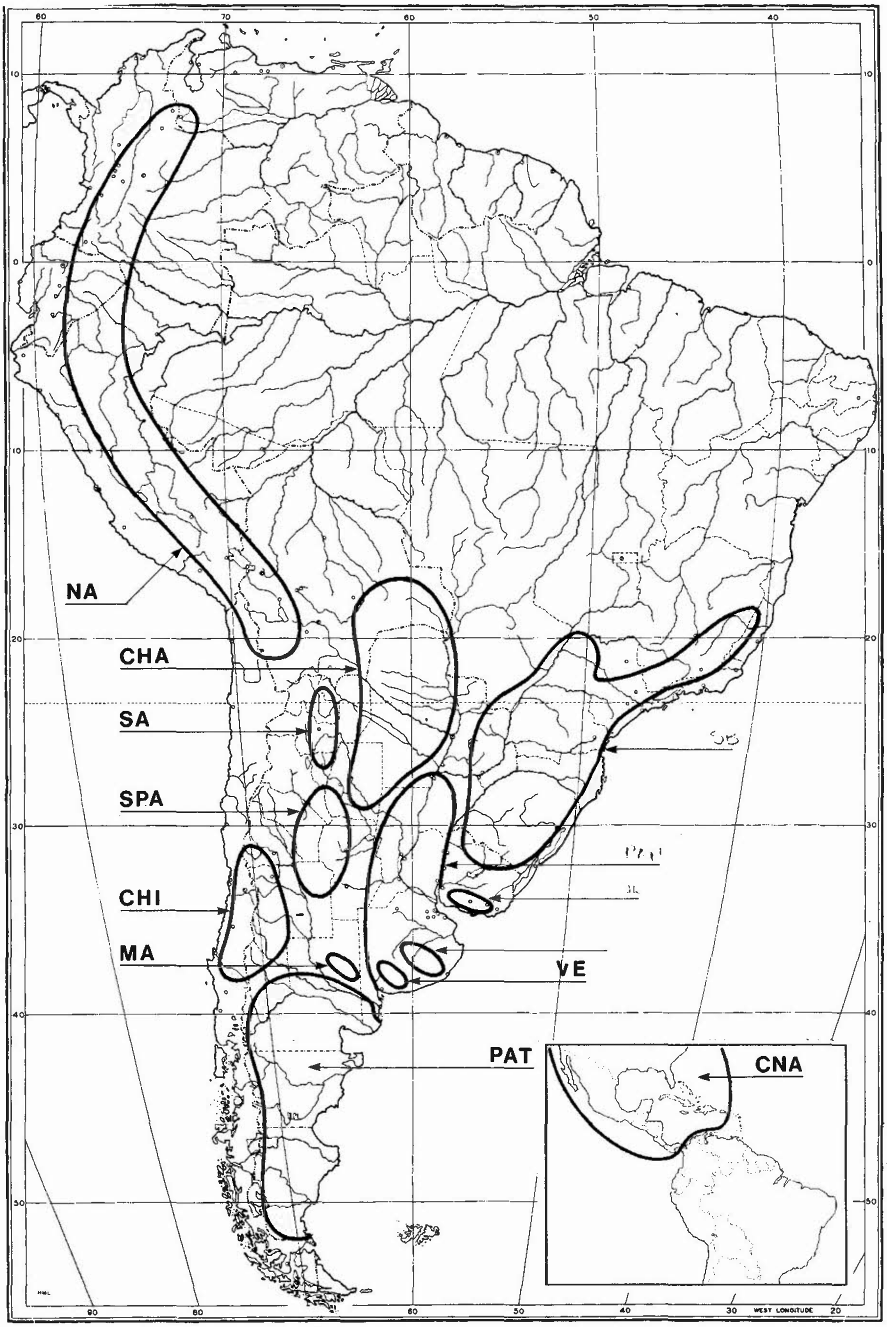

NA
CHA
SA
SPA
CHI
MA
VE
PAT
CNA
SB
WEST LONGITUDE

Fig. 1. Areas of endemism considered in the historical biogeographic analysis: CHA = Chaco; CHI = Central Chile; MA = Mahuidas; NA = Northern Andes; CNA = Central and North America; PAM = Pampa; PAT = Patagonia; SA = Sierras Subandinas; SB = Southern Brazil; SPA = Sierras Pampeanas; TA = Tandilia; UR = Uruguay; VE = Ventania.

(7) *Patagonia* (PAT): semidesert east of the southern Andes to the Atlantic coast in Argentina, approximately between 35° and 55° south latitude (Cabrera & Willink 1973).
(8) *Sierras Pampeanas* (SPA): group of mountain ranges in central Argentina, extending in the political provinces of Córdoba, Santiago del Estero, eastern Catamarca, and San Luis. They are 3500 m high and their Precambric rocks were uplifted during Tertiary and Quaternary times (Gordillo & Lencinas 1980, Michaut 1980).
(9) *Sierras Subandinas* (SA): a group of mountain ranges in northwestern Argentina, extending in the political provinces of Salta and Jujuy. They are 3000-5000 m high; the most ancient rocks belong to the Precambric age (Mingramm et al. 1980) and were uplifted in the Tertiary and Quaternary periods.
(10) *Southern Brazil* (SB): subtropical forest that corresponds to the Paranense province of Cabrera & Willink (1973) in southern Brazil (ranging west of Serra do Mar to central Rio Grande do Sul), northeastern Argentina, and eastern Paraguay.
(11) *Tandilia* (TA): or "Sierras Septentrionales", a group of mountain ranges east of Buenos Aires province. They are 500 m high, and represent the most ancient mountains in Argentina dated from 2200 m. y. ago, in the Proterozoic (Teruggi & Kilmurray 1975, 1980).
(12) *Uruguay* (UR): prairie with endemic taxa, and low mountain ranges. It corresponds to the eastern Uruguayan province (Castellanos & Pérez Moreau 1944, Chebataroff 1960), situated in the south of Brazil (southern Rio Grande do Sul) and Uruguay.
(13) *Ventania* (VE): or "Sierras Australes" a group of moutain ranges southwest of Buenos Aires province. They are 900-1000 m high, and the geological age corresponds to 490 m. y. ago, in the Paleozoic (Llambías & Prozzi 1972, Harrington 1980).

Taxa analyzed

The units of study (Table 2) were species and infraspecific taxa of Asteraceae inhabiting Tandilia and Ventania. The distributional data were taken from the specimens' labels of the herbarium of Departamento Científico de Plantas Vasculares (Herbarium LP), Museo de La Plata, Argentina and from the literature. The number of specimens analyzed are ca. 2500. Each specimen was correctly identified prior to the extraction of data. Checklists (Troiani & Steibel 1999, Zuloaga & Morrone 1999, Cabrera et al. 2000, Peter 2000) and floristic treatments of the province of Buenos Aires (Cabrera 1963, Cabrera & Zardini 1978), and revisionary studies were taken also into consideration. For nomenclature purposes we followed Zuloaga & Morrone (1999). Adventicious (e.g., *Anthemis cotula, Matricaria recutita, Sonchus asper*), cultivated (e.g., *Ci-chorium intybus*), naturalized (e.g., *Artemisia velortorum, Sonchus oleraceous*) or cosmo-politan (e.g., *Solidago chilensis, Taraxacum officinale*) species were not taken into consi-deration.

Panbiogeography (compatibility track method)

Croizat postulated that earth and life evolve together (Croizat 1958), meaning that geographic barriers evolve together with biotas. The panbiogeographic approach (Croizat 1958, 1981) consists of plotting distributions of organisms on maps, connecting their separate distributional areas together with lines called individual tracks. As an example, some of the 112 individual tracks produced in this study of Asteraceae inhabiting Tandilia and/or Ventania and other areas are illustrated (Figs. 2-3). When individual tracks coincide, the resulting summary lines are considered gene-ralized tracks, which indicate the pre-existence of ancestral biotas, that become fragmented by tectonic and/or climatic changes.

Table 1. Taxa endemic to Tandilia and Ventania with the main references.

Taxa	Tandilia	Ventania	References
PLANTAE			
ASTERACEAE			
Baccharis rufescens Spreng var. *ventanicola* Cabrera		X	Cabrera 1963
Baccharis tandilensis Speg.	X		Cabrera 1963
Hieracium burkartii Sleumer	X	X	Cabrera 1963
Hieracium chacoense (Zahn) Sleumer		X	Cabrera 1963
Hieracium tandilense Sleumer	X		Cabrera 1963
Senecio leucopeplus Cabrera		X	Cabrera 1963
S. tandilensis Cabrera	X		Cabrera 1963
S. bravensis Cabrera	X		Cabrera 1963
S. ventanensis Cabrera		X	Cabrera 1963
Stevia satureiafolia (Lam.) Lam. var. *ventanensis* Cabrera		X	Cabrera 1963
BRASSICACEAE			
Rorippa ventanensis Cabrera		X	Boelcke 1967
Sisymbrium ventanense Boelcke		X	Boelcke 1967
BROMELIACEAE			
Dyckia remotiflora Otto & Dietr. var. *tandilensis* (Speg.) Cabrera	X		Cabrera 1968
Tillandsia bergeri Mez	X		Cabrera 1968
CACTACEAE			
Gymnocalycium platense (Speg.) Britton & Rose var. *platense*		X	Zuloaga & Morrone 1999
Gymnocalycium platense (Speg.) Britton & Rose var. *ventanicola* (Speg.) R. Kiesling		X	Zuloaga & Morrone 1999
FABACEAE			
Adesmia bonariensis Burkart	X		Burkart 1967
A. pampeana Speg.		X	Burkart 1967
A. pseudogrisea Burkart		X	Burkart 1967
Astragalus argentinus Manganaro	X	X	Burkart 1967
Lathyrus hookeri G. Don f. *albiflora* (Kuntze) Burkart	X		Burkart 1967
Mimosa rocae Lorentz & Niederl.	X	X	Burkart 1967
Vicia montevidensis Vogel f. *oblonga* Burkart	X		Burkart 1967
V. setifolia Kunth var. *bonariensis* Burkart	X	X	Burkart 1967
IRIDACEAE			
Cypella herbertii (Lindl.) Herb. subsp. *wolffhuegeli* (Hauman) Ravenna	X	X	Ravenna 1968
Sisyrinchium junceum E. Mey. subsp. *lainezii* (Hicken) Ravenna	X	X	Ravenna 1968
PLANTAGINACEAE			
Plantago bismarckii Niederl.		X	Pontiroli 1965
Plantago tandilensis (Pilg.) Rahn	X		Pontiroli 1965
POACEAE			
Bromus bonariensis Parodi & J. A. Cámara		X	Cámara H. 1970
Festuca ventanicola Speg.		X	Cabrera 1970
Piptochaetium calvescens Parodi		X	Torres 1970a
Poa iridifolia Hauman	X	X	Torres 1970b
Setaria vaginata Spreng. var. *tandilensis* Nicora	X		Nicora 1970
Stipa ventanicola Cabrera & Torres		X	Cabrera & Torres 1970
POLYGALACEAE			
Polygala ventanensis Grondona		X	Fabris 1965
SOLANACEAE			
Nierembergia tandilensis (Kuntze) Cabrera	X	X	Cabrera 1965
ANIMALIA			
BOTHRIURIDAE			
Bothriurus voyati Mauri		X	Maury 1973
IGUANIDAE			
Liolaemus gracilis spp.	X		Vega & Bellagamba 1990
Liolaemus sp.	X		Vega & Bellagamba 1990
Prystidactylus casihuatiensis		X	Kristensen & Frangi 1995
LEPTOTYPHLOPIDAE			
Leptotyphlops munoai Orejas Miranda	X	X	Vega & Bellagamba 1990
Melanophryniscus stelzneri subsp. *montevidensis* Philippi	X		Vega & Bellagamba 1990

The compatibility track method herein applied, developed by Craw (1988), is based on the concept of distributional compatibility (Connor 1988, Craw 1989). In this method, individual tracks are treated as biogeographic hypotheses of locality or distribution area relationship. Two or more individual tracks are regarded as being compatible with each other only if they are the same pairwise comparison or if one track is a subset of the other (i.e., tracks are either included within or replicated by one another). It basically consists of constructing a matrix (areas vs. tracks), where each entry is 1 or 0 depending on whether the track is present or absent in each area, and using a compati-bility analysis program to find the largest clique(s) of compatible tracks. The method involves finding a simple form of spanning tree linking localities or distribution areas. This tree is constructed from the largest clique of compatible distributions in a distributional compatibility matrix and is identified as a generalized track. If more than one largest clique or several cliques of considerable size are found, then a hypothesis of existence of several generalized tracks linking the localities or distribution areas in more than one way can be considered. Alternatively, the intersection (i.e., those tracks common to all the largest cliques) of the largest cliques can be identified as a generalized track (Craw 1990). For more details and other applications of this method see Craw (1988, 1989), Morrone & Crisci (1990, 1995), Craw et al. (1999) and Crisci et al. (2000). The analysis of the data matrix of 13 areas of endemism vs. distributional data of 112 taxa (Table 3) was carried out with SECANT 2.2 (Salisbury 1999). SECANT is a program for identifying all groups of cladis-tically compatible characters. We treated our tracks as binary characters ordered with absence as the "ancestral" state for each (= outgroup with all zeros).

Parsimony analysis of endemicity (PAE)

Parsimony analysis of endemicity or PAE (Rosen 1988, Rosen & Smith 1988) is an approach of historical biogeography that led to identify the distributional pattern of organisms. It classifies localities, quadrats or areas (which are analogous to taxa) by their shared taxa (which are analogous to characters) according to the most parsimonious solution (Morrone & Crisci 1995, Crisci et al. 2000). The method was originally proposed by Rosen (1988) using localities as study units.

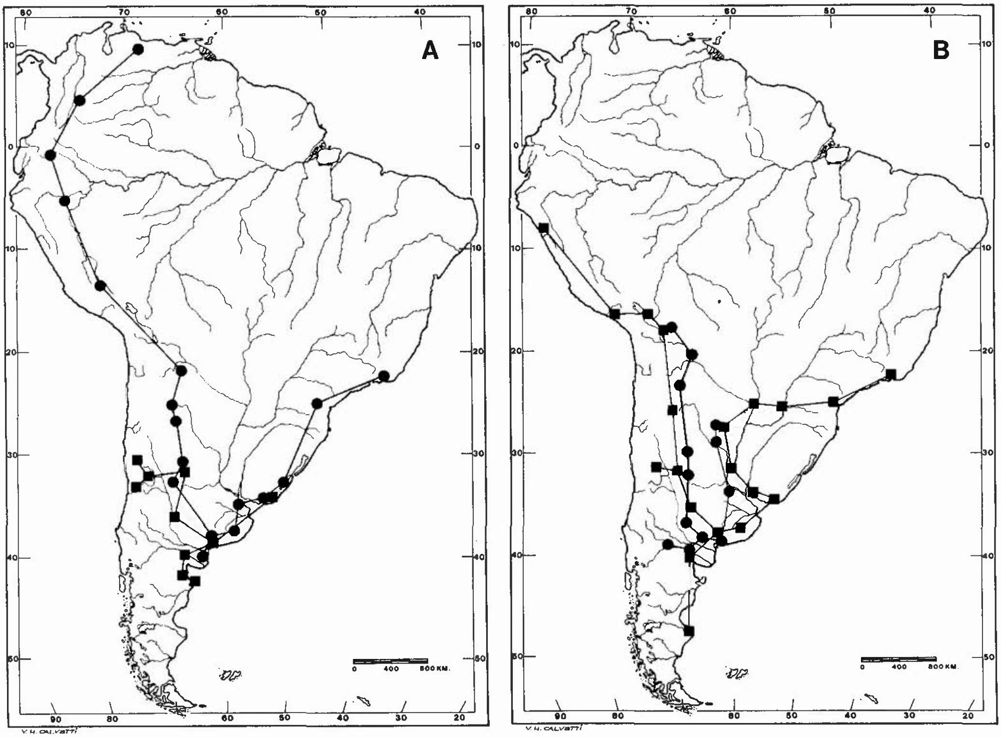


Fig. 2 A-B. Individual tracks. A, *Achyrocline satureioides* (●), *Baccharis crispa* (■); B, *B. ulicina* (●), *Conyza bonariensis* (■).

Table 2. Species of Asteraceae from Tandilia and Ventania and other areas of endemism considered in the study. Taxa with the same areas of endemism have been indented. Areas of endemism for each taxa are indicated in Table 3.

1. *Achyrocline satureioides* (Lam.) DC.
2. *Acmella decumbens* (Sw.) R. K. Jansen var. *affinis* (Hook. & Arn.) R. K. Jansen
3. *Aster squamatus* (Spreng.) Hieron.
4. *Baccharis artemisioides* Hook. & Arn.
5. *B. articulata* (Lam.) Pers.
6. *B. crispa* Spreng.
7. *B. gilliesii* A. Gray
8. *B. spicata* (Lam.) Baill.
9. *B. stenophylla* Ariza
10. *B. triangularis* Hauman
11. *B. tridentata* Vahl var. *subopposita* (DC.) Cabrera
12. *B. trimera* (Less.) DC.
13. *B. ulicina* Hook. & Arn.
14. *Bidens laevis* (L.) Britton, Sterns & Poggenb.
15. *Chaptalia exscapa* (Pers.) Baker var. *exscapa*
16. *C. ignota* Burkart
17. *C. integerrima* (Vell.) Burkart
18. *C. piloselloides* (Vahl) Baker
19. *C. runcinata* Kunth
20. *C. sinuata* (Less.) Baker
    21. *Baccharis coridifola* DC.
    22. *Conyza sumatrensis* (Reitz.) E. Walker
23. *Chuquiraga erinacea* D. Don subsp. *erinacea*
24. *Conyza bonariensis* (L.) Cronq. var. *bonariensis*
25. *C. floribunda* Kunth
26. *C. monorchis* (Griseb.) Cabrera
    27. *Holocheilus brasiliensis* (L.) Cabrera
    28. *Mikania periplocifolia* Hook. & Arn.
    29. *Pamphalea heterophylla* Less.
    30. *Podocoma hieracifolia* (Poir.) Cass.
31. *Conyza primulifolia* (Lam.) Cuatrec. & Lourteig
32. *C. serrana* Cabrera
33. *Eupatorium buniifolium* Hook. & Arn. var. *buniifolium*
34. *E. bupleurifolium* DC.
35. *E. macrocephalum* Less.
    36. *Chevreulia sarmentosa* (Pers.) S. F. Blake
37. *Eupatorium squarrulosum* Hook. & Arn.
    38. *Baccharis gnaphalioides* Spreng.
    39. *Micropsis spathulata* (Pers.) Cabrera
40. *Facelis retusa* (Lam.) Sch. Bip. subsp. *patula* Beauv.
41. *F. retusa* (Lam.) Sch. Bip. subsp. *retusa*
    42. *Gaillardia megapotamica* (Spreng.) Baker var. *scabiosoidea* (Arn. ex DC.) Baker
43. *Flaveria haumanii* Dimitri & Orfila
    44. *Stuckertiella peregrina* Beauv.
45. *Gaillardia megapotamica* (Spreng.) Baker var. *megapotamica*
    46. *Berroa gnaphalioides* (Less.) Beauv.
47. *Gamochaeta americana* (Mill.) Wedd.
48. *G. argentina* Cabrera
49. *G. falcata* (Lam.) Cabrera
    50. *G. subfalcata* (Cabrera) Cabrera
51. *Gamochaeta filaginea* (DC.) Cabrera
52. *G. platensis* (Cabrera) Cabrera
53. *G. stachydifolia* (Lam.) Cabrera
54. *Gnaphalium cabrerae* S. E. Freire
    55. *Hypochaeris pampasica* Cabrera
56. *Gnaphalium cheiranthifolium* Lam.
57. *G. gaudichaudianum* DC.
58. *G. leucopeplum* Cabrera
59. *Grindelia aegialitis* Cabrera
60. *G. brachystephana* Griseb.
61. *G. pulchella* Dunal var. *discoidea* (Hook. & Arn.) A. Bartoli & Tortosa
62. *G. ventanensis* A. Bartoli & Tortosa
63. *Gutierrezia gilliesii* Griseb.
64. *Helenium radiatum* (Less.) Seckt
65. *Hieracium palezieuxii* Zahn
66. *Hyalis argentea* D. Don ex Hook. & Arn. var. *latisquama* Cabrera
    67. *Trichocline sinuata* (D. Don) Cabrera
68. *Hypochaeris petiolaris* (Hook. & Arn.) Griseb.
69. *Hysterionica jasionoides* Willd.
70. *Conyza bonariensis* (L.) Cronq. var. *angustifolia* (Cabrera) Cabrera
71. *Hysterionica pinifolia* (Poir.) Baker
    72. *Hypochaeris rosengurttii* Cabrera var. *pinnatifida* (Speg.) Cabrera
73. *Lucilia acutifolia* (Poir.) Cass.
74. *Microgynella trifurcata* (Less.) Grau
75. *Noticastrum marginatum* (Kunth) Cuatrec.
76. *Perezia multiflora* (Humb. & Bonpl.) Less. subsp. *sonchifolia* (Baker) Vuilleum.
    77. *Eupatorium commersonii* (Cass.) Hieron.
    78. *Hypochaeris grisebachii* Cabrera
79. *Pluchea sagittalis* (Lam.) Cabrera
    80. *Senecio grisebachii* Baker var. *grisebachii*
81. *Podocoma hirsuta* (Hook. & Arn.) Baker
    82. *Conyza blakei* (Cabrera) Cabrera
    83. *Eupatorium subhastatum* Hook. & Arn.
    84. *Noticastrum diffusum* (Pers.) Cabrera
85. *Senecio arechavaletae* Baker
86. *S. bonariensis* Hook. & Arn.
87. *S. grisebachii* Baker var. *subincanus* Cabrera
    88. *S. ostenii* Mattf.
89. *Senecio montevidensis* (Spreng.) Baker
    90. *Micropsis australis* Cabrera
91. *Senecio pampeanus* Cabrera
92. *S. pulcher* Hook. & Arn.
    93. *Eupatorium tanacetifolium* Gillies ex Hook. & Arn.
    94. *Grindelia buphthalmoides* DC.
    95. *Hypochaeris variegata* (Lam.) Baker
    96. *Sommerfeltia spinulosa* (Spreng.) Less.
97. *Senecio subulatus* D. Don ex Hook. & Arn. var. *erectus* Hook. & Arn.
98. *Soliva pterosperma* (Juss.) Less.
99. *Stevia satureiifolia* (Lam.) Lam. var. *patagonica* Hieron.
100. *S. satureiifolia* (Lam.) Lam. var. *satureiifolia*
101. *Thelesperma megapotamicum* (Spreng.) Kuntze
     102. *Noticastrum argentinense* (Cabrera) Cuatrec.
103. *Vernonia echioides* Less.
     104. *Acmella decumbens* (Sw.) R. K. Jansen var. *decumbens*
     105. *Baccharis genistifolia* DC.
     106. *Criscia stricta* (Spreng.) Katinas
     107. *Eupatorium tweedianum* Hook. & Arn.
     108. *Hypochaeris megapotamica* Cabrera
     109. *Senecio selloi* (Spreng.) DC.
     110. *Stevia multiaristata* Spreng.
111. *Vernonia flexuosa* Sims.
112. *Zexmenia buphthalmiflora* (Lorentz) Ariza

Craw (1988) and Cracraft (1991) presented a variation of the method using areas of endemism as study units to identify the hierarchical information contained in the geographical distribution of organisms to establish area relationships. In this method a data matrix of endemism areas by taxa is constructed, and the presence of a taxon in an area is coded as 1 and its absence as 0. A parsimony algorithm is applied to the matrix to obtain a cladogram(s). PAE cladograms represent nested sets of areas, in which terminal dichotomies represent two areas between which the most recent biotic interchange has occurred (Morrone & Crisci 1995). In this analysis the same areas and data matrix (Table 3) used in the panbiogeographic approach were taken into consideration. The analysis was carried out with PAUP* version 4.0 beta 2 (Swofford 1999), applying the branch-and-bound option. A strict consensus tree was constructed based on the results generated from PAUP*. As proposed by Rosen (1988), the cladogram was rooted with a hypothetical area coded all zeros.

RESULTS

Panbiogeography (compatibility track method)

Based on the data matrix (Table 3), the combination of the individual tracks resulted in four largest cliques (generalized tracks) of 30 individual tracks each one (Fig. 4 A-D). The intersection of 27 individual tracks (identified with the numbers 3, 20, 21, 23, 25, 26, 27, 28, 29, 30, 36, 37, 38, 81, 82, 83, 84, 87, 88, 103, 104, 105, 106, 107, 108, 109, 110 in Table 2) common to the four largest cliques is identified as the fifth clique or generalized track (Fig. 4 E). In this way, six individual tracks (5, 40, 41, 63, 64, and 98 in Table 2) are combined in groups of three with the 27 individual tracks to form the four cliques of 30 individual tracks mentioned above.

Five trees connecting the areas can be constructed from the five cliques, as follows (Fig. 4):

Clique A: ((((((((TA, UR), SB), PAM), VE), SPA), CHA), SA), NA), PAT, CHI), supported by the 30 individual tracks 3, 5, 20, 21, 23, 25, 26, 27, 28, 29, 30, 36, 37, 38, 40, 41, 81, 82, 83, 84, 87, 88, 103, 104, 105, 106, 107, 108, 109, 110 (Fig. 4 A).

Clique B: ((((((((TA, UR), SB), PAM), VE), SPA), SA), CHA), NA), CHI, PAT), supported by the 30 individual tracks 3, 5, 20, 21, 23, 25, 26, 27, 28, 29, 30, 36, 37, 38, 63, 64, 81, 82, 83, 84, 87, 88, 103, 104, 105, 106, 107, 108, 109, 110 (Fig. 4 B).

Clique C: ((((((((TA, UR), SB), PAM), VE), SPA), CHA), SA), CHI) NA, PAT), supported by the 30 individual tracks 3, 20, 21, 23, 25, 26, 27, 28, 29, 30, 36, 37, 38, 40, 41, 81, 82, 83, 84, 87, 88, 98, 103, 104, 105, 106, 107, 108, 109, 110 (Fig. 4 C).

Clique D: ((((((((TA, UR), SB), PAM), VE), SPA), SA), CHA), CHI), NA, PAT), supported by the 30 individual tracks 3, 20, 21, 23, 25, 26, 27, 28, 29, 30, 36, 37, 38, 63, 64, 81, 82, 83, 84, 87, 88, 98, 103, 104, 105, 106, 107, 108, 109, 110 (Fig. 4 D).

Clique E: ((((((((TA, UR), SB), PAM), VE), SPA), SA, CHA) NA, PAT, CHI), supported by the 27 individual tracks 3, 20, 21, 23, 25, 26, 27, 28, 29, 30, 36, 37, 38, 81, 82, 83, 84, 87, 88, 103, 104, 105, 106, 107, 108, 109, 110 (Fig. 4 E).

Mahuidas and Central and North America are the only areas that appear in none of these pattern of relationships in the five generalized tracks obtained.

Due to the fifth clique (E) represents the intersection of 27 individual tracks common to the four largest cliques, it was selected to show the taxa supporting the areas relationship (Fig. 4 E):

(1) (TA,UR). Based on *Senecio grisebachii* var. *subincanus* (individual track 87) and *S. ostenii* (track 88).

(2) ((TA,UR), SB). Based on *Eupatorium squarrulosum* (track 37), *Baccharis gnaphalioides* (track 38), and *Micropsis spathulata* (track 39).

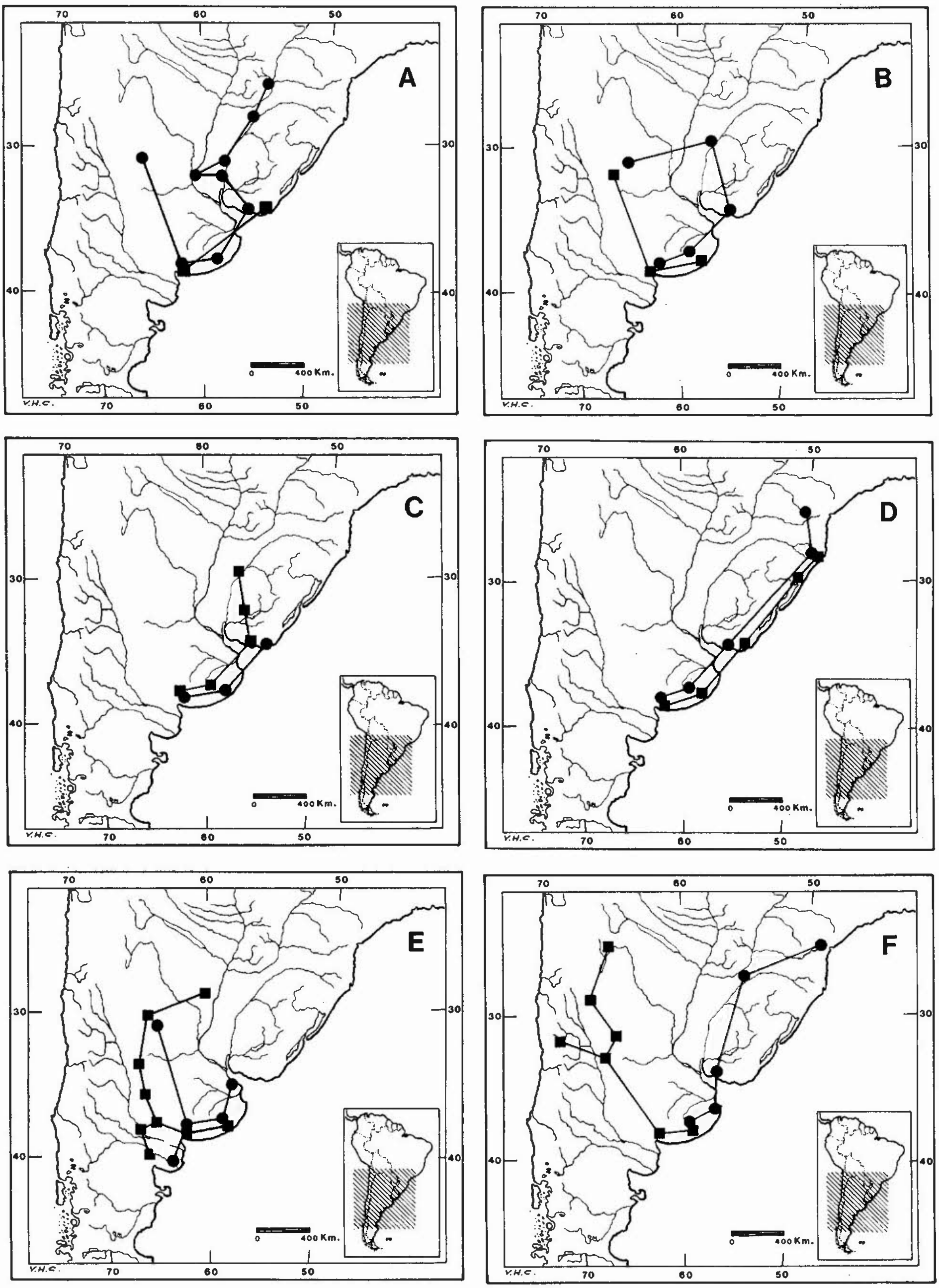
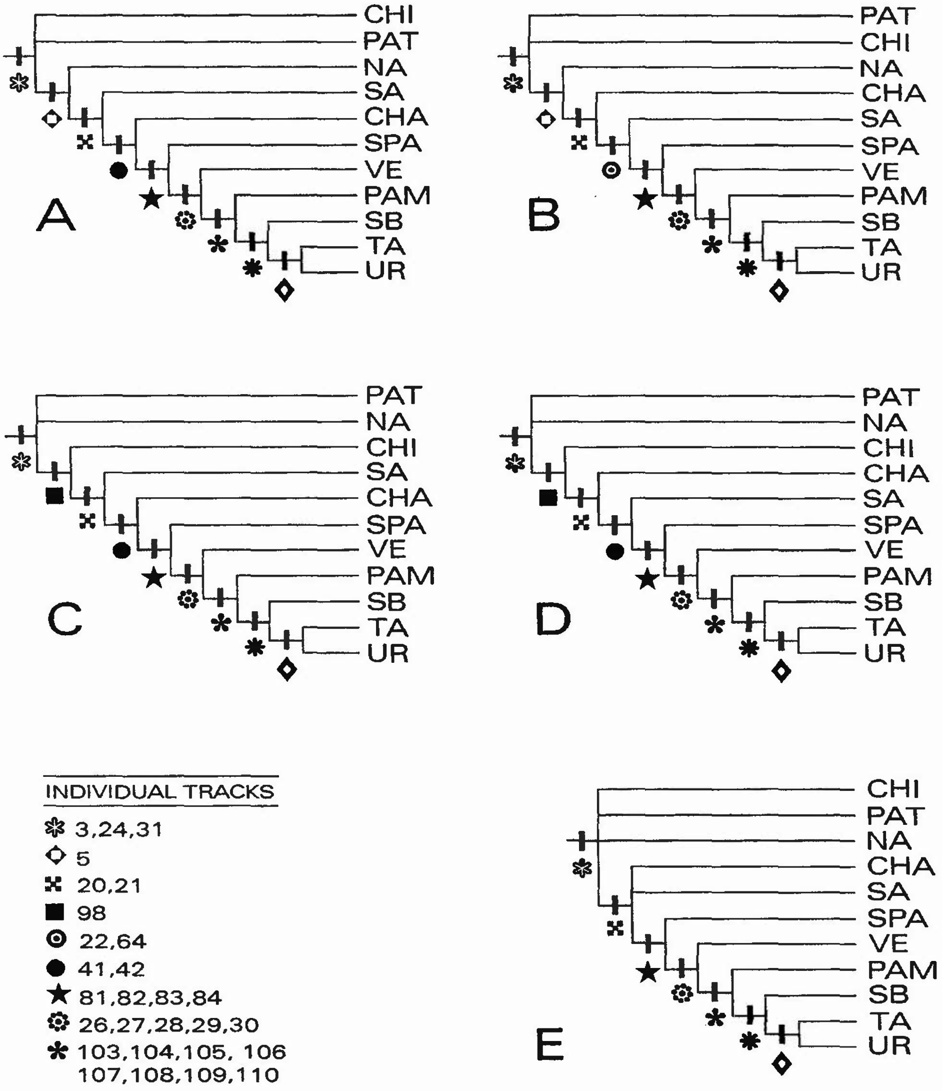


Fig. 3 A-F. Individual tracks. A, *Podocoma hirsuta* (●), *Senecio arechavaletae* (■); B, *Hieracium palezieuxii* (●), *Hyalis argentea* var. *latisquama* (■). C, *Hysterionica pinifolia* (●), *Perezia multiflora* subsp. *sonchifolia* (■); D, *Senecio pulcher* (●), *Sommerfeltia spinulosa* (■); E, *Senecio bonariensis* (●), *Senecio pampeanus* (■); F, *Vernonia echioides* (●), *Zexmenia buphtalmiflora* (■).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INDIVIDUAL TRACKS
❃ 3,24,31
◇ 5
⌘ 20,21
■ 98
◎ 22,64
● 41,42
★ 81,82,83,84
❁ 26,27,28,29,30
✱ 103,104,105, 106 107,108,109,110
✸ 37,38,39
◇ 87,88

Fig. 4. A-E. Cliques obtained in the compatibility track method after applying SECANT 2.2, showed as cladograms. A-D, Four largest cliques each supported by 30 individual tracks. E, Clique obtained by the intersection of 27 individual tracks common to the four largest cliques. The table shows the individual tracks or the sets of individual tracks, represented by symbols, that are superimposed onto the cladograms (see Table 2 for numbers corresponding to taxa names and Table 3 for individual tracks). CHA = Chaco; CHI = Central Chile; NA = Northern Andes; PAM = Pampa; PAT = Patagonia; SA = Sierras Subandinas; SB = Southern Brazil; SPA = Sierras Pampeanas; TA = Tandilia; UR = Uruguay; VE = Ventania.

(3) (((TA,UR), SB), PAM). Based on *Vernonia echioides* (track 103), *Acmella decumbens* (track 104), *Baccharis genistifolia* (track 105), *Criscia stricta* (track 106), *Eupatorium tweedianum* (track 107), *Hypochaeris megapotamica* (track 108), *Senecio selloi* (track 109), and *Stevia multiaristata* (track 110).
(4) ((((TA,UR), SB), PAM), VE). Based on *Conyza monorchis* (track 26), *Holocheilus brasiliensis* (track 27), *Mikania periplocifolia* (track 28), *Panphalea heterophylla* (track 29), and *Podocoma hieracifolia* (track 30).
(5) (((((TA,UR), SB), PAM), VE), SPA). Based on *Podocoma hirsuta* (track 81), *Conyza blakei* (track 82), *Eupatorium subhastatum* (track 83), and *Noticastrum diffusum* (track 84).

Parsimony analysis of endemicity

The analysis of the data matrix (Table 3) with PAUP* generated four area cladograms (Fig. 5 A-D) with 263 steps, c.i.= 0.426, and r.i. = 0.663. The strict consensus of the four trees (Fig. 5 E) shows the following area relationships: (Mahuidas (Patagonia (Chile (Sierras Subandinas (Sierras Pampeanas (Ventania (Pampa (Southern Brazil – Tandilia – Uruguay)))))))). The remaining areas: Chaco (CHA), Central and North America (CNA), and northern Andes (NA) do not show resolved relationships with the other areas in the consensus.

Comparison of both methods

The comparison of the results obtained applying panbiogeography (compatibility track method) and parsimony analysis of endemicity to the areas under study shows a coincidence in the relationships of Sierras Pampeanas (SPA), Ventania (VE), Pampa (PAM), Southern Brazil (SB), Tandilia (TA), and Uruguay (UR).
The areas relationship PAM-SB-SPA-TA-UR-VE conform a main distributional pattern strongly supported by the two approaches applied in this study, and represented in Fig. 6 as a generalized track. Both methods show that Tandilia is closer to Uruguay, southern Brazil, and Pampa than to Ventania. On the other hand, PAE and panbiogeography resulted in different relationships of the remaining other areas with the main distributional pattern. PAE shows that Sierras Subandinas (SA) (Fig. 5 A-E) are related to this pattern, whereas panbiogeo-graphy shows that Sierras Subandinas can be directly related to it (Fig. 4 B, D) or cannot be directly related (Fig. 4 A, C); PAE shows Chaco (CHA) as not closely related to the pattern (Fig. 5 A-E), whereas panbiogeography shows CHA connected to it (Fig. 4 A-E); PAE shows Mahuidas (MA) and Central and North America (CNA) not closely related to the pattern (Fig. 5 A-E), and panbiogeography shows these last two areas very distantly related to it (for this reason they are not indicated in the results).

DISCUSSION

The main distributional pattern connecting Tandilia and Ventania with southern Brazil, Pampa, Uruguay, and Sierras Pampeanas obtained through the compatibility track method and PAE partially agree with others authors' hypotheses.
A biotic migratorial route from the Andes to Brazil, through Sierras Pampeanas, sierras of Buenos Aires, sierras of Uruguay, and Planalto and sierras of Brazil was postulated many years ago by Hicken (1918-1919) and Brade (1942). Frenguelli (1950) gave the name of peripampasic orogenic arc (*arco peripampásico serrano*) to the biotic corridor constituted by Sierras Pampeanas, Mahuidas, and Tandilia. Ringuelet (1956) postulated that the province of Buenos Aires constitutes a composite area due to the presence of two types of fauna: one related to the Subtropical domain (Guaianian-Brazilian), and the other related to the Austral region (Andean-Patagonic, or Chilean-Patagonic).

Table 3. Data matrix (areas vs. individual tracks) for the compatibility track analysis and for the parsimony analysis of endemicity. CHA = Chaco; CHI = Central Chile; CNA = Central and North America; MA= Mahuidas; NA = Northern Andes; OUT = outgroup; PAM = Pampa; PAT = Patagonia; SA = Sierras Subandinas; SB = Southern Brazil; SPA = Sierras Pampeanas; TA = Tandilia; UR = Uruguay; VE = Ventania. Absence = 0; presence = 1. Number of taxa correspond to those of Table 2.

	1	2	3	4	5	6	7	8	9	10	11	
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12
OUT	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	00
CHA	0010101100	1011000011	1001000000	1000000000	1100000000	0100001001	0000000011	0000000011	0000000000	0000000100	0000000000	10
CHI	0010011000	0001000000	0011100000	1010000000	0011111100	1001111100	1010000011	0010000000	0000000000	0000001110	1100000000	01
CNA	0000000000	0001000010	0000000000	0000110000	0000001000	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000	00
MA	0101000000	0010000000	0000100000	0010000001	0000000100	1010010100	0010000011	0000000000	0000000000	1000000010	1100000000	00
NA	1010100000	0111101010	0001100000	1000000000	0000001000	0000000000	0000000000	0010100000	0000000000	0000000000	0000000000	00
PAM	1011111110	1111111111	1101111111	1011110000	1111111111	1111101011	1011111111	0011011111	1111010011	1000001101	1111111111	10
PAT	1010011011	0010000000	0011100000	1000000001	0011111000	1011101101	1010000011	0000000000	0000010011	1000001010	1100000000	00
SA	1111101000	1111001001	1111100000	1111110000	0011001011	0000001100	0011000011	0010100011	0000000000	0000001100	0000000000	01
SB	1010100100	1101101111	1101111111	1111111110	1100111011	1010011101	1001000000	0011000011	1111000011	0111111100	0011111111	10
SPA	1111111111	0011101011	1111100000	1010110001	1111111111	1011111100	1011111011	0011100011	1111010011	1000001111	1100000000	01
TA	1111100100	1001111011	1101111111	1111111111	1100001100	1010010011	1101100000	1110011111	1111011100	1111110111	0011111111	11
UR	1011110110	1101110111	1101111111	1111001110	1100111111	1010011100	1001100100	1111011111	1111101111	0111110100	1111111111	10
VE	1011111011	1110101101	1111111111	1111110001	1111111111	1111111101	0111111111	1111111100	1111110011	1111110111	1100000000	01

Sota (1967, 1972, 1973, 1985) in his analyses of the ferns growing in Tandilia and Ventania, concluded that the pteridological flora of these mountain ranges have four origins: Austral-Antarctic, Andean-Pampean, Austrobrazilian, and Endemic. According to his studies the Buenos Aires' mountain ranges constitute an intermediate orofilous station in the migratorial routes between the Andean-Pampean or the Austral-Antarctic flora, and the Austrobrazilian flora. Maury (1973) established, on the basis of the scorpions inhabiting Tandilia and Ventania, nearly the same kind of relationships with other areas as showed by Sota: with the Subtropical domain, Central domain (Sierras Pampeanas), and Patagonian and Central Chilean domains.

The studies based on ferns and scorpions show a link between Tandilia and Ventania with the Austral region, a kind of relationship not found here for Asteraceae. Although some Asteraceae inhabiting Tandilia and Ventania occur in Patagonia, Central Chile and Mahuidas, they do not constitute or are included in a generalized track. It is possible that different taxonomic groups such as scorpions, ferns and Asteraceae have undergone different historical processes that led to their actual distributional pattern.

The relationships among the areas of the main distributional pattern found in this study show that Tandilia is closer to Uruguay and southern Brazil than to Ventania. Although Tandilia and Ventania are geographically close to each other, the geological evidence suggests that both mountain ranges resulted from independent geological processes at different geological times. According to Ramos (1989), Ventania was the result of the collision of a Patagonian block that drifted from the south and accreted to Gondwanaland (ca. 360-440 m.y. ago). Tandilia, on the other hand, was a part of the Río de La Plata craton (together with northeast Argentina, east Paraguay, Uruguay and southeast Brazil) before the end of the Precambrian (530-570 m.y. ago). Due to the family Asteraceae is believed to have originated in South America in the Tertiary, during the Oligocene (38 m.y.ago) (Stuessy et al. 1996), two geological events may have played a significant role in the Asteraceae evolution and distribution in Tandilia and Ventania and related areas, the uplift of the Andes and the Pleistocene glaciations.

During late Cenozoic (10-5 m.y. ago) the uplift of the Andes together with the development of cold offshore currents have been associated with a diversification of habitats and evolutionary opportunities for the biota (Darlington 1968, Axelrod et al. 1991) especially for the Asteraceae (Funk et al. 1995, Stuessy et al. 1996).

From the Miocene (25-5 m.y. ago) to Pliocene (5-1 m.y. ago) the climate was drying in southern South America caused by the slowly raising of the Andean chain and the cold Humboldt current that intensified aridity. The last phase of the Andean orogeny in the upper Pliocene caused additional uplift of Sierras Pampeanas and Sierras Subandinas (Taylor 1991), that had started their uplift with the climax of the Andean cordillera raising during the Tertiary.

Finally, during the Pliocene and Pleistocene in the Quaternary period, glaciations caused dry and wet cycles that caused fragmentation and differentiation of the populations (Simpson Vuilleumier 1971, Simpson 1975). Semiarid vegetation extended into the continent, e.g., to the south Patagonia, north of Atacaman desert, Chaco, and Monte, in the core of South America, and the cerrado and caatingas in central and northeastern Brazil, respectively (Prado & Gibbs 1993). This may resulted in an eventual separation of populations in more elevated regions, restricted now to rocky and loose soils. The main distributional pattern found in this study connecting the mountain ranges of southern Brazil, Uruguay, Tandilia, Ventania and Sierras Pampeanas, and the Asteraceae endemicity found in Tandilia and Ventania could be explained as a consequence of these events.

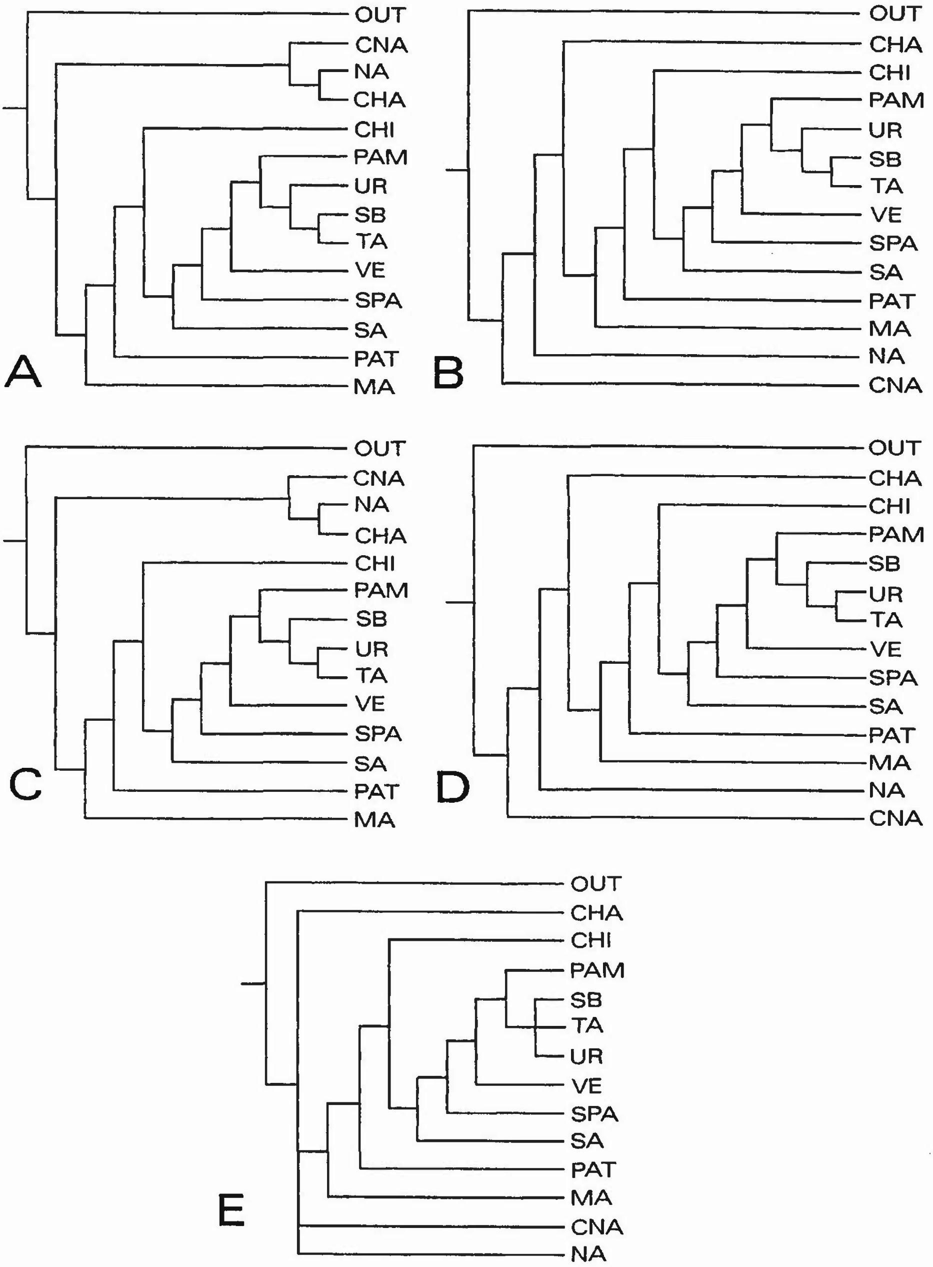
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Fig. 5. A-E, Cladograms obtained after applying parsimony analysis of endemicity after applying PAUP*. A-D, Four area cladograms. E, Strict consensus of the four cladograms. CHA = Chaco; CHI = Central Chile; MA = Mahuidas; NA = Northern Andes; CNA = Central and North America; PAM = Pampa; PAT = Patagonia; SA = Sierras Subandinas; SB = Southern Brazil; SPA = Sierras Pampeanas; TA = Tandilia; UR = Uruguay; VE = Ventania.

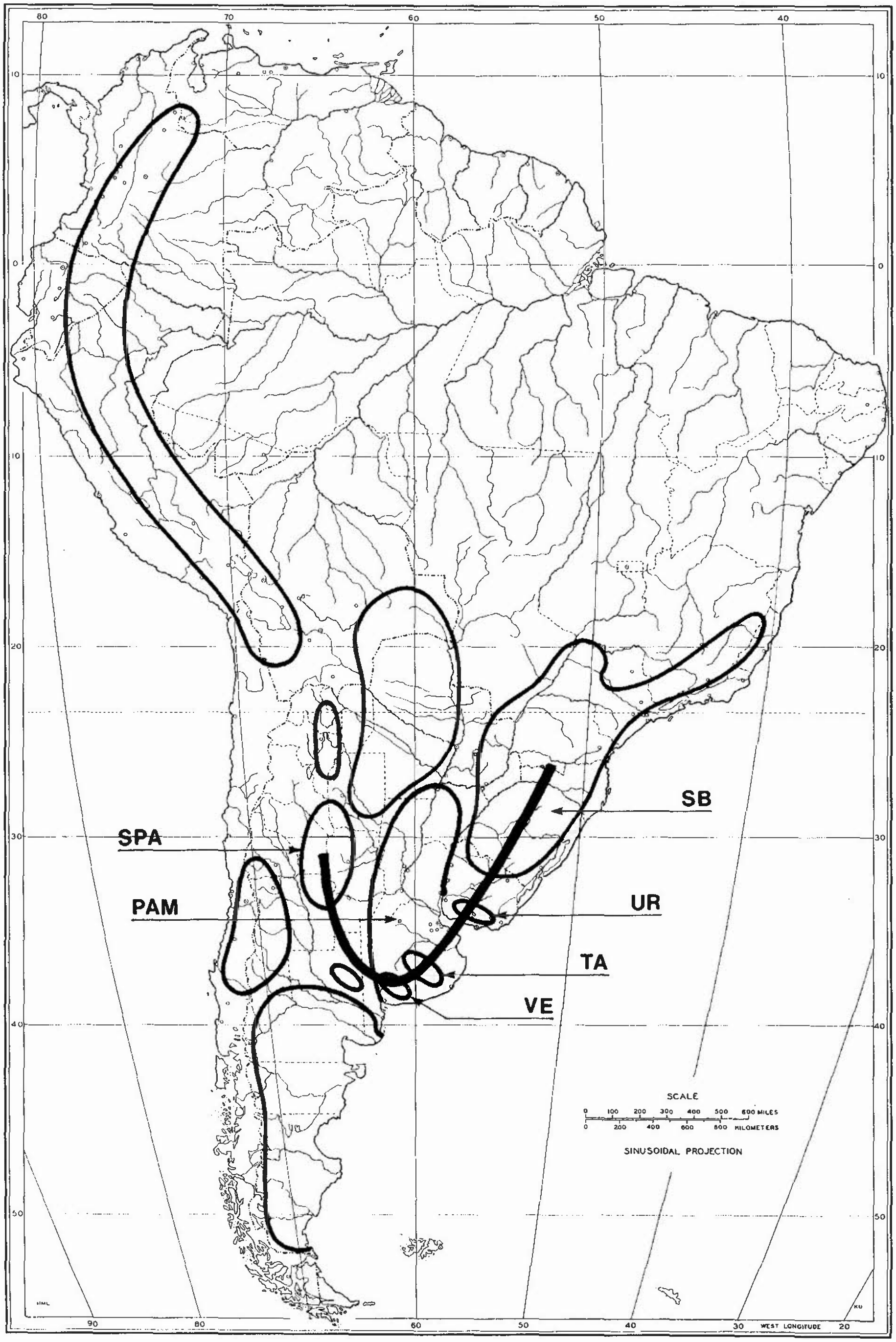
SPA
PAM
SB
UR
TA
VE
SCALE
0 100 200 300 400 500 600 MILES
0 200 400 600 800 KILOMETERS
SINUSOIDAL PROJECTION
WEST LONGITUDE

Fig. 6. Distributional pattern of relationships among areas based on Asteraceae taxa, and represented as a generalized track. PAM = Pampa; SB = Southern Brazil; SPA = Sierras Pampeanas; TA = Tandilia; UR = Uruguay; VE = Ventania.

In summary, it is probable that the evolution of Asteraceae in Tandilia and Ventania was mainly affected by Tertiary and Quaternary geologic events. As a result, this biota shows a high level of diversity, many endemic taxa, and closer relationships with southern Brazil, Uruguay, Pampa, and Sierras Pampeanas rather than with other areas of America. The discon-tinuous pattern, i.e., occurring in elevated areas surrounding a core area of Chaco and Monte vegetation, is what one would expect under vicariance due to dry conditions, although dis-persal is taken also as a common and impor-tant distributional event. Further correlations with analyses of other plant and animal taxa will determine the generality of the pattern shown by Asteraceae.

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